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LEENA AHOLA

Effects of Social and Physical Housing Environment on the Welfare in Silver Foxes (*Vulpes vulpes*)

Doctoral dissertation

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ABSTRACT

Farmed silver foxes (*Vulpes vulpes*) are usually weaned and separated from their mothers at the age of seven-eight weeks. After this the cubs are first kept in larger sibling groups but subsequently they are raised either in pairs or singly in cages measuring 115 cm long x 105 cm wide x 70 cm high. The current housing circumstances do not necessarily fulfil foxes' species-specific needs for social and locomotor behaviour and, thus, the foxes' welfare may not be optimal.

In the present study, the effects of different social and physical housing environments on behavioural and physiological as well as on production-related welfare indices were evaluated. The effects of the social environment were assessed by either changing group composition (including or excluding the mother) or group size (one, two, four or five siblings within a group). Spatial requirements were studied by changing the quality (seminatural enclosures or wire-mesh cages) and the quantity (space per individual fox varying between 0.6-28 m^2) of the living area. Furthermore, the impact of different housing environments on human-animal relations was defined. In clarifying the effects of these two factors under farm conditions, the knowledge of the behaviour and adaptations of the wild red fox (the silver fox is a colour mutation of the red fox) were applied.

The cubs that were weaned directly into single living performed more stereotyped behaviour in early winter than the cubs that were housed either in pairs or in quartets. Although it seems that for young farmed foxes social contact does act as an environmental enrichment and can improve their welfare, the situation is somewhat different at the time of natural dispersal. When the mother of the cubs was included into the group the welfare of her cubs, and especially her male cubs, was disrupted due to the prevention of their inherent tendency to disperse from their mother's living area. Overall, even between the siblings, aggressive encounters increased and the individuals within each group tended to avoid each other with the advance of autumn. Though it possibly provided the foxes with some sense of control of their living environment, available space had only minimal effects on the foxes. The need of foxes to adopt territorial behaviour may have been eliminated in farm conditions where there is plentiful and stable food supplies. However, constructions enriching the living areas (e.g. platforms, separating walls in cage systems) are important for foxes, providing them with opportunities to avoid group members and to survey their surroundings. The quantity of space further affects the expression of human-animals relations. In large enclosures, foxes are desocialised from human and may eventually become feral. Both social and physical environments affect the quality of furs of foxes. A soil floor as such impairs the fur quality. Keeping silver foxes in groups leads to increased social tension and aggressiveness with the consequence of an increased incidence of bite wounds and poorer fur quality, especially in group-housed females. Decreasing the space allocation in cage conditions also decreases the fur quality.

In conclusion, the welfare of farmed silver foxes can be promoted by altering their social conditions according to their developmental stage. Furthermore, quality rather than quantity of the living area is the crucial factor for the welfare of farmed silver foxes.

Universal Decimal Classification: 591.6, 636.93, 636.083.6
CAB Thesaurus: animal behaviour; animal housing; animal physiology; animal welfare; fur faming; fur quality; social environment; stocking density; *Vulpes vulpes*

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Kuopio, September 2002

ABBREVIATIONS

ACTH	Adrenocorticotrophic hormone
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
C-C	Cortisol-creatinine
CTSH	Constant Territory Size Hypothesis
EC	European Convention
GAST	Gastrocnemius muscle
GPI	Group preference index
HPA	Hypothalamic-pituitary-adrenal
RDH	Resource Dispersion Hypothesis
SDH	Succinate-dehydrogenase
SIH	Stress-induced hyperthermia
TIH	Territory Inheritance Hypothesis

LIST OF ORIGINAL PUBLICATIONS

This dissertation includes the following papers referred to in the text by their Roman numerals I-IV:

I Ahola L, Mononen J: Family break-up in farmed silver foxes (*Vulpes vulpes*) housed in enlarged cage systems as families. Acta Ethol 4: 125-127, 2002

II Ahola L, Harri M, Kasanen S, Mononen J, Pyykönen T: Effect of family housing of farmed silver foxes (*Vulpes vulpes*) in outdoor enclosures on some behavioural and physiological parameters. Can J Anim Sci 80: 427-434, 2000

III Ahola L, Harri M, Mononen J, Pyykönen T, Kasanen S: Welfare of farmed silver foxes (*Vulpes vulpes*) housed in sibling groups in large outdoor enclosures. Can J Anim Sci 81: 435-440, 2001

IV Ahola L, Mononen J, Pyykönen T, Mohaibes M, Rekilä T: Effects of group size and space allocation on physiological, behavioural and production-related welfare parameters in farmed silver fox cubs. Submitted

This thesis also contains previously unpublished data. Unpublished data from the experiments presented in II and III are based on the material and methods of the original publications and marked with superscript ^{u} (i.e. II^{u}, III^{u}).

CONTENTS

1 INTRODUCTION

During the recent years, public concern about the welfare of farmed animals has greatly increased. Among other farmed species, this concern extends also to farmed fur animals including the two farmed fox species, the silver fox (*Vulpes vulpes*) and the blue fox (*Alopex lagopus*, or *Vulpes lagopus*, see Macdonald and Geffen 2001). For these species, concern has been directed at the cage environment where the foxes are raised (Nimon and Broom 2001; see European Commission 2001). Traditional fox cages (usually 115 x 105 x 70 cm, L x W x H) are considered as being too barren and small for the animals. Hence, the possibilities for farmed foxes to move and perform species-specific behaviour may be challenged. Furthermore, because foxes are generally raised either singly or in pairs, they may not be able to show the social behaviour typical to the species. It is also considered that, due to the short history of farming practice, farmed foxes cannot be domesticated animals in the same way as dogs, horses and cattle etc. This suggests that farmed foxes housed in cage conditions are not necessarily adapted to their current physical and social environment and have difficulties in tolerating the proximity of humans.

Animal protection has been taken into account in several specific acts and general regulations concerning fur animal husbandry (European Convention, EC, 1999; Ministry of Agriculture and Forestry 1999). In Finland, general requirements concerning animal welfare are laid down in the Act on Animal Protection (247/1996), Statute on Animal Protection (396/1996) and Statute on the Transport of Animals (491/1996). More detailed provisions on the requirements for the keeping, care, treatment and handling of fur animals have been included in the Ministry of Agriculture and Forestry Decision on animal welfare requirements for fur animals (16/VFD/1999). These requirements are analogous to the recommendations concerning fur animals given by the EC (1999).

The EC's (1999) recommendations concerning fur animals include also a call for the development of husbandry systems and research on the welfare of farmed foxes. Accordingly, many welfare-related studies on the topics proposed by the EC have been carried out in Finland and in other Nordic countries using both farmed fox species: year-round nest boxes (e.g. Jeppesen and Pedersen 1991, 1992; Pedersen and Jeppesen 1993; Harri et al 1998; Mononen et al 1998b), observation platforms (e.g. Harri et al 1991; Korhonen and Niemelä 1996b, c; Mononen 1996; Mononen et al 1997, 1998a, b) and different floor materials and cage sizes (e.g. Korhonen and Niemelä 1997; Harri et al 1999, 2000; Korhonen et al 2001a, c, d) (see also Nimon and Broom 2001). Some of the results gained from earlier studies induced by the EC's (1999) recommendations have already led to legislative changes in fur farming practice, e.g. use of resting platforms or nest boxes (Ministry of Agriculture and Forestry 1999).

The EC's (1999) recommendations further state that 1) "Whenever this is a part of the normal behaviour pattern of the species and improves the welfare of the individuals, animals shall be able to see conspecifics and be able to show social investigation and behaviour associated with the maintenance of social structure.", 2) "The design…of enclosures and accommodation for fur animals shall at all times allow them…to carry out normal locomotor behaviour…" and 3) "Shared space systems involving tunnels and removable walls between cages…shall be considered.". With regard to the possibilities of farmed foxes to enjoy social behaviour and adequate locomotor behaviour, there already exists a great number of appropriate results in farmed blue foxes (e.g. Korhonen and Alasuutari 1991, 1992, 1994, 1995; Korhonen and Niemelä 1996a; Korhonen et al 1991, 1999, 2000, 2001a, c, d; Ahola et al 2000, 2002). In contrast, in silver foxes there is a paucity of analogous research.

The recommendations laid down by the EC (1999) led to a start of a three-year project called "Development of alternative housing environments for farmed foxes with a special reference to animal welfare". This project was carried out as a co-operation between University of Kuopio, MTT Agrifood Research Finland, Finnish Society for the Protection of Animals and Finnish Fur Breeders' Association. One of the main aims of this project was to "provide a stimulating environment to enable animals to fulfil their biological needs" (EC 1999) by giving the foxes the possibility to behave socially (group housing) and to exercise more (larger space for locomotor behaviour). In designing the alternative housing systems for foxes, both the practicality and the species' social and spatial behaviour in the wild were taken into account. The present study is based mainly on this project and on the physiological, behavioural and production-related results obtained from silver foxes during their growing seasons (June-January) over the years of this project.

2 REVIEW OF THE LITERATURE

2.1 Silver fox farming - past and present

The red fox and its other colour form, the silver fox, were the first animals farmed for furs (Forester and Forester 1973). The first foxes were caught from the wild in Canada in 1890's, and descendants of these animals were brought to Europe almost 100 years ago. At that time, foxes were housed generally in groups in outdoor enclosures with up to 100 m^2 of floor area. Enclosures were soil floored and an underground den was dug into the soil for reproducing animals. The intention was to raise farmed foxes in conditions that would resemble the conditions of the species in the wild. However, it was soon realised that in these conditions endoparasites were found in almost every fox, fights between the individuals were common and cub mortality was high in the damp, cold underground dens (Smith 1928). Furthermore, the foxes did not habituate to humans (Smith 1928) although the farmers already at that time acknowledged the importance of positive human-animal relations (Bakken and Moe 2001). Therefore, it was considered that, to ensure better health conditions for the foxes, foxes should be raised on an elevated wire floor with a limited number of animals within a housing system (Broberg and Puustinen 1931).

At present, the minimum space requirements for farmed foxes are laid down by both the EC (1999) and the Ministry of Agriculture and Forestry, Finland (16/VFD/1999). The minimum space for a single adult fox is 0.8 m^2 and for a single adult with its cubs 2.0 m^2. For two juveniles, the minimum space after weaning is 1.2 m^2. If more than two cubs are kept together, an extra 0.5 m^2 for each additional cub must be provided. The minimum dimensions of the fox cage have been designated as 75 x 100 x 70 cm (W x L x H). These space requirements shall be applied to new and replaced accommodations, and by the end of year 2010 they will apply to all accommodations.

In Finland, the present practice is that silver foxes are farmed in wire-mesh cages (usually 115 x 105 x 70 cm, L x W x H) (European Commission 2001). Furthermore, according to the requirements of the Ministry of Agriculture and Forestry (1999), cages are furnished with an elevated platform made of plastic covered wire mesh.

As adults both male and female silver foxes are kept singly in one cage (European Commission 2001). In April-May, the vixen gives birth in a cage furnished with a wooden nest box. The cubs are kept with their mother until the time of weaning, which takes place at the time when cubs are approximately eight weeks old (in June-July). After that, cubs may first be kept in larger sibling groups but later in autumn (in July-August) they are often separated to live predominantly in pairs, or singly. The pairs comprise generally of a male and a female sibling.

2.2 Outlines of welfare definitions

The scientific outlines specifying the concept of animal welfare can be grouped into three different approaches, namely nature-based, feelings-based and functioning-based (Duncan and Fraser 1997; Fraser et al 1997).

The nature-based approach stresses that animals should be allowed to behave in their 'natural' ways and have the freedom to perform most types of their natural behaviour repertoire (see Duncan and Fraser 1997). According to this approach, "to promote the welfare of animals we need to raise them in ways that respect their natures" (Rollin 1993). However, despite appearing more romantic to humans as outsiders, a life in nature is not necessarily better than a life under human care (Dawkins 1980; Hart 1985). Furthermore, there is no evidence indicating that possible behavioural or physiological differences between the wild and farmed animals *per se* show that the farmed animals are actually suffering (Dawkins 1980).

The feelings-based approach stresses the importance of feelings as "welfare is solely dependent on what animals feel" (Duncan 1996). According to this approach, the term 'welfare' can be applied only to higher, sentient animals, i.e. to animals that are capable to feel, e.g. mammals and birds (Manteca 1998). The welfare of an animal is good if it is free from fear, pain, hunger and other negative states and experiences comfort, pleasure and other positive states (Dawkins 1990; Webster 1995; Duncan and Fraser 1997).

Since feelings are an animal's own private experiences (Dawkins 1980) some scientists have found it hard or even impossible to measure feelings (Gonyou 1993), and have placed different emphasis on subjective experiences and biological function (see Duncan and Fraser 1997). The functioning-based approach suggests that good welfare is indicated by normal or satisfactory functioning of physiological and behavioural processes. If an animal is subjected to noxious circumstances for a long period of time, this may lead to inadequacies in the animal's behavioural and physiological coping systems (e.g. Moberg 1985, 2000; Broom and Johnson 1993). In these terms, the functioning-based approach to the welfare can be defined as "an animal's state as regards its attempt to cope with its environment" (Fraser and Broom 1990). Coping difficulties, i.e. poor welfare, can become evident as behavioural and physiological stress symptoms. These symptoms include e.g. abnormal behaviour and elevated levels of stress hormones in blood as well as morbidity and mortality, which all can be used as measures of welfare (e.g. Fraser and Broom 1990; Broom & Johnson 1993).

The three approaches, although putting different emphasis on feelings, functioning and nature, are, however, closely related to each other (Fraser et al 1997). The animal is a mix of both genetic adaptations gained during its evolution and domestication and phenotypic adaptations gained during its own ontogeny. Feelings are also a product of evolution and they contribute to fitness (Dawkins 1998). From an evolutionary point of view, subjective feelings have evolved to strengthen fitness-promoting behaviour and can be considered to indicate to the animal the success of its coping strategies (Dawkins 1990, 1998). Ultimately, stress and poor welfare could be perceived as reduced fitness of an animal (Fraser and Broom 1990; Broom and Johnson 1993). However, measuring animals' fitness under farming conditions is often impossible, e.g. in determining fitness on non-reproducing farmed animals housed in different living conditions. Therefore, distinct tools are used to adjust the welfare status of the animals. These tools include several physiological and behavioural indicators that are easier to measure and that presumably can demonstrate whether fitness of the animal is reduced or not, e.g. as a consequence of inferior living conditions. In other words, when an animal has needs, i.e. requirements to obtain a particular resource or respond to a particular stimulus, physiological and behavioural responses are elicited in order to meet these requirements. If the requirements are met, the animal is able to cope with its environment, i.e. it has control of its mental and bodily stability (Broom and Johnson 1993). If a need cannot be satisfied despite the animal's motivational state and this state is prolonged, or occurs with high frequency or intensity, then the outcome may be poor welfare associated with measurable changes in the animal's physiological and behavioural function (e.g. Broom and Johnson 1993; Moberg 2000).

Thus, Fraser et al (1997) combined all the three approaches into an integrative model for defining the concept of animal welfare. They also pointed out how this model helps to determine how animals under human husbandry ought to be treated so that their welfare can be assured. According to this model, welfare problems may arise when the adaptations possessed by an animal do not fully correspond to the challenges posed by its current environment. Problems in the welfare of animals can, thus, occur if animals hold adaptations that serve no function in their current living environment, if there are environmental challenges to which the animals do not possess the corresponding adaptations or if adaptations, even if corresponding to environmental challenges, prove to be inadequate in the current environment.

Despite the number of welfare measurement methods proposed and used during the last decades, assessing welfare in a scientific manner is not simple (e.g. Rushen 1991; Rushen and de Pasillé 1992; Duncan and Fraser 1997), and no single parameter can unambiguously define the welfare status of an animal (e.g. Rushen 1991; Rushen and de Pasillé 1992; Broom and Johnson 1993). However, there is a firm consensus that the welfare of an animal can be measured (e.g. Fraser and Broom 1990; Broom and Johnson 1993; Duncan and Fraser 1997; Fraser et al 1997; Ewing et al 1999) but, in order to assess the welfare of animals, a set of different physiological and behavioural parameters need to be used even within each experiment (Dawkins 1980; Broom and Johnson 1993; Mason and Mendl 1993; European Commission 2001; Korhonen et al 2001b). Furthermore, one has to be aware that, even if it were possible to assess animal welfare by applying objective scientific methods, human society's present values, technology, economics, regulations and knowledge still impinge on the interpretation of the outcome of the assessments and on how animal welfare is perceived (Fraser and Leonard 1993).

With regard to farmed fur animals, the history of farmed foxes has in practice included all three approaches of how the animals ought to be treated to ensure their welfare (and also profitable production). During the early years of fur farming practice, the farmers reasoned, perhaps intuitively, that satisfactory biological function of the animals could be achieved by raising them in conditions which resembled to a greater or lesser extent their conditions in the wild (nature-based approach, Duncan and Fraser 1997). However, the decision to raise foxes in groups in soil floored enclosures ended in difficulties in the animals' physiological and behavioural responses (e.g. high cub mortality, increased aggressiveness and incidence of diseases). Therefore, it was soon considered better to raise foxes in cage conditions with a limited number of animals included in each housing system (functioning-based approach). At present, a normal physiological and behavioural functioning of animals still plays an important role in defining the welfare of farmed foxes, as revealed by the main defined problems in the current farming practice, e.g. foxes' fear of human and failures in reproduction. However, at present, it is also emphasised that proper function, in the sense that animal production is profitable, is not sufficient to ensure that the animals' welfare is guaranteed, and that farmed foxes, being sentient animals capable of feelings, can suffer if their living conditions are poor (feelings-based approach).

2.3 Wild red fox

The knowledge of the behaviour of the species in the wild facilitates a better understanding of the behaviour of the species under farm conditions (Mendl and Newberry 1997) because the behaviour of farmed animals still closely resembles that of their wild conspecifics (see Rushen et al 1999). Therefore, social behaviour and spatial organisation of the wild red fox are reviewed below.

2.3.1 Social organisation

In nature, group living evolved because it gave the individuals a higher fitness than the individuals would have achieved when living alone (Gittleman 1989; Alcock 1993; Manning and Dawkins 1998). The benefits gained by group living include both the exploitation of food resources and detection of and defence against possible predators (Macdonald 1983; Gittleman 1989; Alcock 1993; Mendl and Newberry 1997). Furthermore, group formation enhances reproductive success (e.g. access to individuals of the other sex, presence of non-reproducing 'helpers', see Gittleman 1989; Moehlman 1989), facilitates learning (Macdonald 1983; Gittleman 1989; Fraser and Broom 1990; Nicol 1995) and increases collective resistance against a harsh environment (Gittleman 1989). However, grouping has also its disadvantages. In larger groups, the chance of being detected by potential predators as well as transmission of diseases and parasites increases whereas the amount of feed intake for an individual may decrease (Gittleman 1989; Alcock 1993; Mendl and Newberry 1997; Manning and Dawkins 1998).

In the wild, all canids have a trend to form a monogamous pair bond at the time when rearing their cubs (e.g. Kleiman 1977; Eisenberg 1989; Moehlman 1989). Therefore, the mating pair has been considered to be the basic social unit also in the red fox (e.g. Voigt and Macdonald 1984; Moehlman 1989). However, and possibly due to the great ability to adapt to different circumstances, variable social structures among red foxes have been found (see Sandell 1989). On the one hand, red foxes have some times been viewed as being rather solitary with no or only limited co-operation with conspecifics, except during the mating season (Lloyd 1975; Cavallini 1996). On the other hand, although the red fox is basically monogamous, this monogamy may deviate to polygyny (Vergara 2001), e.g. due to changes in food availability (Zabel and Taggart 1989) (see Cavallini 1996). Accordingly, there is also evidence that the social groups of red foxes may consist of a male and one to five subordinate females that are often related to each other (Macdonald 1979, 1980, 1981, 1983; von Schantz 1981, 1984; Hersteinsson and Macdonald 1982; Voigt and Macdonald 1984; Doncaster and Macdonald 1991; Poulle et al 1994). Social groups may also be comprised of more than one male (Harris and Smith 1987). Although organised into social groups, close interactions between adult foxes within a group are low (Macdonald 1983; Poulle et al 1994).

In the wild red fox, the benefits of living in groups may not be the same as for other carnivores. The red fox is quite small in its body size and preys on species smaller than itself (Harris and Lloyd 1991). Therefore, there seems to be only little or no benefits of grouping at least with regard to exploitation of food resources. Furthermore, despite the finding that in smaller carnivore species group defence is expected to be more common than in larger species (Gittleman 1989), no communal defence has been detected in the red fox (Cavallini 1996). Therefore, as red foxes live often in forests or habitats with at least some cover where co-operation in hunting, in exploitation of food or in group defence may not be feasible (Gittleman 1989), the primary benefit of group living for the wild foxes may be alloparental care of the young (Macdonald 1983).

Hypotheses of why small carnivores live in social groups, despite there being only infrequent or minor benefits of social ties (Macdonald 1983), have been proposed by Macdonald (the Resource Dispersion Hypothesis, RDH, 1983), von Schtanz (the Constant Territory Size Hypothesis, CTSH, 1984) and Lindström (the Territory Inheritance Hypothesis, TIH, 1986).

Macdonald's RDH suggests that "the smallest home range with an economically defensible configuration which will reliably support a pair of foxes (on a bad night or a bad year) may sometimes support additional foxes due to a patchily distributed but rich supply of food"

(Macdonald 1983). In other words, for the solitary foragers, e.g. red foxes, group size is determined by the abundance of food.

According to von Schantz (1984) social groups among red foxes may arise during years when food resources are rich, similarly to Macdonald's RDH (1983). However, CTSH suggests that if the food supply fluctuates with a period shorter than the average life span of an individual, then the animal will defend a territory of the year with the lowest food resources available. If food supply should increase in some year, then the territory of the 'bottle-neck year' will support also adult offspring and they are allowed to stay in their home range.

Lindström's (1986) TIH, in contrast to RDH and CTSH, does not presuppose anything about the stability of the structure of the food environment. Lindström proposes that social groups of related individuals should arise because there are benefits of staying in the home territory for both the primary pair and the offspring of the pair. The original territory holders, by allowing their offspring to stay, ensure that the territory will be inherited by carriers of their own genes, and the offspring, by staying at home, assure themselves a better survival chance in a more familiar environment.

Accordingly, although it seems to be less advantageous for smaller, rather than larger, canids to live in groups (Gittleman 1989; Moehlman 1989) the red fox lives at least occasionally in some kind of social unit. The population group size is affected by the habitat and by the abundance of food resources (Hersteinsson and Macdonald 1982; Macdonald 1983; Sandell 1989; Harris and Lloyd 1991; Macdonald et al 1999). The ability to form social bonds between the conspecifics has been suggested to be one of the causes for (female biased) group formation (Bekoff 1977, 1989; Harris and White 1992). In the red fox, both adult and juvenile females are more closely bonded to their social group (Harris and White 1992; Allen and Sargeant 1993) and are more tolerant towards each other (Fox 1987) than male foxes. In wintertime and during the breeding season, the general aggressiveness increases (White and Harris 1994). Adult male foxes attend to care of their young but the degree of male contribution to cub care has not been thoroughly demonstrated (Lampio 1972; Lloyd 1975; Fox 1987; Moehlman 1989; Vergara 2001). Males are more likely to live a more solitary life (Fox 1987) and to disperse during their first years of life (e.g. Harris and Trewhella 1988; Baker and Harris 2000).

The ultimate reasons for dispersal may be inbreeding avoidance, competition for mates and competition for resources (Greenwood 1980). In foxes, the proximate reasons for dispersal behaviour have been explained either by social cohesion (Bekoff 1977) or by social subordination (Christian 1970) of the members of the family. The social subordination hypothesis (Christian 1970) suggests that aggression from dominant animals leads to dispersal of subdominants. The social cohesion hypothesis (Bekoff 1977), in contrast, points out that the individuals most prone to leave are those unable to develop, maintain and receive affiliative bonding behaviour from their siblings, i.e. both the most submissive and the most dominant individuals. The main dispersal time occurs during September-December (e.g. Lloyd 1975; Storm and Montgomery 1975; Allen and Sargeant 1993), i.e. after the cubs have reached their independence at the age of 6-8 months (see Gittleman 1989; Nimon and Broom 2001). Male foxes typically disperse first and further (e.g. Hersteinsson and Macdonald 1982; Harris and Trewhella 1988; Baker and Harris 2000) while females may stay in their natal territory with their mother, e.g. acting as non-breeding ‘helpers’ for the reproducing vixen (e.g. von Schantz 1981; Hersteinsson and Macdonald 1982; Macdonald 1983). The distance dispersed from the natal den is unaffected by population density, and dispersal has, therefore, been regarded as a strong innate behaviour in red foxes, and especially in males (Allen and Sargeant 1993). When dispersing, littermates tend to disperse in the same direction (Harris and Trewhella 1988; Allen and Sargeant 1993).

2.3.2 Spatial organisation

The red fox has been viewed as being highly flexible in its preferences for different kinds of habitats (Poulle et al 1994). It has the widest geographical distribution of any present carnivore, occupying habitats as different as tundra, desert, forest and agricultural landscapes as well as cities (e.g. Hersteinsson and Macdonald 1982; Harris and Smith 1987).

The spatial organisation of the wild foxes is determined by the animals’ territoriality and by their use of home ranges (Doncaster and Macdonald 1991; Alcock 1993). Territory can be defined as an area defended by the animal whereas a home range is an undefended area used regularly for routine activities (Frafjord 1992; Alcock 1993). Home ranges of wild red foxes vary in their size from 0.1 to 50 km^2 (e.g. Hersteinsson and Macdonald 1982; Novak and Paradiso 1983; Voigt and Macdonald 1984; Pandolfi et al 1997). Red foxes have been considered as being either highly territorial with non-overlapping home ranges (Ables 1969;

Macdonald 1981, 1983; Hersteinsson and Macdonald 1982; von Schantz 1984; Goszczynski 1989; Doncaster and Macdonald 1991, 1997; White et al 1996) or being only slightly territorial (Kolb 1986; Cavallini 1996; Macdonald et al 1999).

The spatial system of the wild red fox, i.e. the size, stability and use of home ranges and territories, varies according to dispersion and availability of food (Hersteinsson and Macdonald 1982; Macdonald 1983; von Schantz 1984; Lovari et al 1994; Macdonald et al 1999). According to Macdonald (1983), territories are just large enough to provide resources for the territory's holders and are, therefore, principally determined by the spatial distribution of resource patches. In other words, if availability (and not necessarily the total amount) of food increases, the size of a territory should decrease.

In sparse habitats (e.g. prairies) home ranges are much larger than in diverse, rich habitats with e.g. plenty of food and suitable resting sites (e.g. cities, suburbs) (e.g. Macdonald 1983; Harris and Lloyd 1991; Lovari et al 1994; Lucherini and Lovari 1996; Macdonald et al 1999). Furthermore, home ranges are smaller at high population densities (family groups per m^2) (Zimen 1984; Trewhella et al 1988; Baker et al 2000) and for juveniles (Adkins and Stott 1998). Younger foxes, further, do not use their ranges equally but restrict their activities to particular sites of their home ranges (Kolb 1986). The sex of the animal, on the other hand, has only a minor impact on the living area of the wild foxes (Poulle et al 1994; Meia and Weber 1995; Lucherini and Lovari 1996; Macdonald et al 1999), though White et al (1996) observed male foxes to employ larger home ranges than females.

2.3.3 Human affiliation

The red fox, with its flexible way of life, inhabits different kinds of areas with respect to its proximity to humans (e.g. Macdonald 1987; Doncaster and Macdonald 1991). Foxes are found in forests with few contacts with humans as well as in city areas where the probability for interacting with humans is more likely. The red fox is said to have a bad reputation among humans in rural areas, due both to the losses it causes to gamekeepers and farmers and to the fact that it is the main vector for the spread of rabies in Central Europe (e.g. Harris and Lloyd 1991). The local circumstances affect the behaviour of the red fox towards humans (Hersteinsson and Macdonald 1982). In areas where red foxes are hunted and considered as more or less noxious animals, foxes often try to keep their distance from humans, whereas for example in Israel, where foxes are largely protected, foxes can become very tame.

2.3.4 Summary

The wild red fox is highly flexible in its living habits. Although basically monogamous, the red fox lives also in groups consisting of a male fox and different aged females that often are closely related to each other (e.g. sisters or offspring of the dominant, reproducing vixen). The amount and availability of food resources are the main factors affecting the number of foxes living within a group and the size of the territory or home range. Female foxes are better adapted to group living while juvenile males are more solitary after leaving their natal area during their first year of life and before finding a mate. The aggressiveness of foxes increases in wintertime and during the breeding season, and adult foxes (especially the males) tend to be more aggressive and less tolerant than juveniles. The wild red fox inhabits areas with both scarce and abundant possibilities for human contact and shows high flexibility also in its relations with humans.

2.4 Designing housing environment for group-housed farmed foxes

2.4.1 Social environment

Social housing is potentially the most powerful way of enriching the lives of animals kept in captivity (Mendl and Newberry 1997). With regard to farmed fur animals, the EC (1999) recommends that “if it is a part of the normal behaviour pattern of the species and improves the welfare of the individuals, animals shall be able to see conspecifics and be able to show social investigation and behaviour associated with the maintenance of social structure”.

Social organisation within a group of animals is illustrated by the group’s physical structure (e.g. group size, age and sex of animals) and social structure (i.e. relationships among group members) as well as by group cohesion (i.e. duration of associations of group members) (Fraser and Broom 1990). In farmed animals, the physical structure of a group is often controlled by man, and animals are usually not able to choose whether to stay or leave the group they are housed in. Therefore, in order to facilitate animal welfare, careful consideration should be carried out in designing group housing of farmed animals. In addition to the present knowledge from the species in the farm environment, the understanding of the species' natural behaviour aids in developing alternative housing systems (Dawkins 1980; Mendl and Newberry 1997) because the behavioural changes occurring during the domestication process are quantitative rather than qualitative (Price 1999).

The number of animals housed together should be limited so that the members of the group are able to recognise each other (Fraser and Broom 1990). This enables the animals to form within-group social hierarchies that, in turn, obviate fighting attributable to undetermined social relations. The greater the number of animals within the group, the higher the number of social contacts and the harder it is to maintain stable social relations (Fraser and Broom 1990). In addition to group size, the composition of groups including age, sex and relatedness of the individuals should be adjusted for the species to guarantee the welfare of group members (Fraser and Broom 1990; Mendl and Newberry 1997).

With regard to farmed silver foxes, there is little data available on how the physical structures of the group can affect foxes' physiological and behavioural profiles. In a Danish study reviewed by Bakken et al (1994), one, two, four or eight silver foxes were housed together. The foxes housed in larger groups had more bites but they also grew better and were more active than the foxes housed in smaller groups or singly. However, no data was available on the sex ratio of the animals or whether the foxes within groups were related to each other. It may be that increased bite damages and increased activity in larger groups were due to placing unfamiliar foxes into the same living area. In the other farmed fox species, the blue fox, a social organisation is readily formed, even in groups comprising of foxes which are not related to each other (Korhonen and Alasuutari 1994, 1995). In groups, adults and males dominate juveniles and females, respectively, and aggressiveness before breeding time is rarely observed.

Adult farmed foxes may be kept in the same accommodation only during their mating or in exceptional circumstances, and when kept together, adequate supervision should be guaranteed (EC 1999). This is understandable because aggressiveness between group-housed adult female and male silver foxes increases at the onset of breeding time on farms (Pyykönen et al 1997). Furthermore, keeping the father of the cubs in the families throughout the growing season is not necessary for the survival of the cubs (Pyykönen et al 1997, 2002).

2.4.2 Physical environment

The size of an animal sets the minimum limits for the physical environment of that animal (physical space requirements, Keeling 1995). However, if animals are kept in groups, more space is needed to allow the animals to interact or to avoid interactions with one another (Fraser and Broom 1990; Keeling 1995; Mendl and Newberry 1997). Group housing of animals inevitably leads to an enlargement of the total living space for the members of a group if one wishes to comply with the minimum space requirements for the species (e.g. fur animals: EC 1999).

More space is also needed to assure that an animal could be able to perform activities demanding movements (dynamic space requirements, Keeling 1995). An appropriate amount of space under farming conditions provides animals with the possibility for locomotor behaviour and freedom of movement. This, in turn, may provide animals with control of their environment, reduce frustration and help animals to maintain their physical condition (Gonyou 1996). Furthermore, additional space enables the addition of enriching furnishings to the farm environment (Nimon and Broom 2001).

In farmed silver foxes, Pedersen and Jeppesen (1998) found that increasing cage size from 1.2 to 9.6 m^2 provides no solutions for improving welfare of individually housed farmed silver foxes. In pair housed blue foxes, the welfare of foxes, measured by several physiological and behavioural responses of the animals, was not unambiguously impaired in 0.5 m^2 cages which are less than a half the size of a standard cage size (1.2 m^2), nor did increasing cage size from the standard size to 15 m^2 result in any marked welfare effects (Korhonen et al 2001c). However, Korhonen et al (2001d) reported that locomotor stereotypy did increase with increasing cage size.

The feeding systems used in group-housed animals should also be carefully designed (Fraser and Broom 1990). Social farm animal species desire to eat simultaneously with conspecifics (Nielsen 1999). For farmed silver foxes, there is no data available of whether the animals are social eaters or not. The wild form of the farmed silver fox, the red fox, is not necessarily social (Cavallini 1996), and co-operation in hunting and searching for food among red foxes is rarely observed. In farmed blue foxes, given a limited amount of feeding places, aggressiveness is most pronounced during and before the feeding times (Korhonen and

Alasuutari 1991, 1992). Providing each animal within a group with a feeding place of its own may be an important key factor in promoting the welfare of individuals within a group (Mendl and Newberry 1997). This may be the case also in silver foxes because both social and spatial organisations observed in natural fox populations are primarily dependent on the dispersion and abundance of food resources (e.g. Macdonald 1983).

When animals are housed in groups, injuries inflicted on each other by aggressiveness can raise serious animal welfare problems (Mendl and Newberry 1997). With regard to farmed foxes, the incidence of injuries may not be solely due to the limited space available since even in the wild with 'unlimited' space many foxes die due to injuries induced during fights (Harris and Smith 1987). Furthermore, to ensure proper welfare for the individual animals housed in groups, special attention should also be paid to the incidence of infectious diseases, because transmission of diseases occurs more readily in group housing compared to individual housing systems (Fraser and Broom 1990).

More important than excessive quantity of space may be the quality of the space (Hansen and Brandt 1989; Fraser and Broom 1990; Stricklin 1995; Nimon and Broom 2001). Animals may use features of their living environment other than the floor area in their perception of the 'pleasantness' of space (Stricklin 1995). These other features may include perimeter of the cage, the existence of corners and hiding places and the social organisation within the living space (Stricklin 1995; Fraser et al 1997). Furthermore, the concept of a preferable environment varies between animal species (e.g. Alcock 1993; Stricklin 1995). In fact, as Stricklin (1995) has suggested, ultimately animals do not have spatial needs but they have species-specific behavioural and physiological needs that can only be met through certain spatial relationships. In farmed silver foxes, these needs have only recently been widely studied (e.g. Jeppesen and Pedersen 1991, 1992; Pedersen and Jeppesen 1993; Mononen 1996; Harri et al 2001). For example, resting platforms may serve as observation places and nest boxes as hiding places for farmed foxes (Mononen 1996). Furthermore, both of these constructions may act as an unspecific environmental enrichment and enhance the foxes' control of their environment (Mononen 1996) and, hence, their welfare (e.g. Broom and Johnson 1993).

In farming systems, where the costs incurred in animal husbandry (e.g. housing systems, feed) and the production gained (e.g. furs) have to be economically defensible, the spatial organisation is a compromise between the costs invested by humans and the benefits gained by animals (Keeling 1995). This cost-benefit system may, in fact, be quite appropriate for the animals because the productivity of an animal is linked to its welfare (Ewing et al 1999). Therefore, it is profitable for a producer to give the animals enough space to fulfil their species-specific needs (see Stricklin 1995). Furthermore, although in the wild territories and home ranges are large, their sizes vary according to the availability of resources, e.g. food and mates (e.g. Macdonald 1983). On the farm, farmers provide the animals with these resources and, therefore, the animals' space requirements may not be the same as in the wild. However, it should be emphasised that in addition to food and mates, farmed animals certainly have also other needs (e.g. need for exploration, e.g. Broom and Johnson 1993) that further affect their spatial requirements.

With respect to the spatial environment, the EC (1999) has provided recommendations for both the quality and quantity of the living space for farmed foxes. According to the EC, the spatial organisation should allow without difficulty a thorough inspection of all animals, give the animals the possibility to conceal themselves from people and from animals, provide the animals with sufficient room to carry out normal locomotor behaviour, to groom themselves, to lie down, to rest, to sleep in natural postures, to stretch their limbs and to rise. Furthermore, barren environments should be avoided, environments should be enriched and shared space systems involving tunnels and removable walls between cages should be considered.

2.4.3 Human-animal relations

Despite the long domestication history, many farm animals may be afraid of people (e.g. Fraser and Broom 1990; Hemsworth 1997). This is the case also with regard of farmed foxes (Bakken et al 1994; Nimon and Broom 2001; see European Commission 2001). Because fear, i.e. an animal's subjective response to the threat protecting the animal from injury, is an undesirable state of suffering and affects the behavioural processes of the animal (Webster 1995; Jones 1997), the animal's fear of humans can have major effects on the stress level of the animals, cause losses in production and create handling problems as well as an increase in the incidence of injuries in both the farmed animals and the humans that take care of the animals (e.g. Broom and Johnson 1993; Rushen et al 1999). Therefore, to reduce the level of fear towards humans experienced by the farmed animals, sufficient amount of human-animal contacts during the animals' life span, and especially during their period of primary socialisation, have to be guaranteed.

In farmed foxes, as in most farmed species (Fraser and Broom 1990), daily care taking leads to social attachment to humans. This attachment can further be encouraged by positive reinforcement, e.g. by giving the foxes pleasant treatments e.g. titbits (Dale and Bakken 1992; Bakken et al 1993; Bakken 1998) (see European Commission 2001). Furthermore, foxes' attachment to humans is possibly even more pronounced if the animals are either handled or given a sufficient amount of early visual experiences with the farm environment during their sensitive period of socialisation (Belyaev et al 1985; Pedersen and Jeppesen 1990; Pedersen 1991, 1992, 1993, 1994; cf. pigs Hemsworth et al 1987; Hemsworth and Barnett 1991, 1992; Paterson and Pearce 1992; cf. hens Barnett et al 1994).

The sensitive period of primary socialisation of silver foxes begins when the cubs are approximately three weeks old and lasts until the age of over nine weeks in populations selected for domestic behaviour (Belyaev et al 1985). Handling silver foxes during this time has been largely successful in reducing the silver foxes' fear reactions towards humans (Tennessen 1988; Pedersen and Jeppesen 1990; Pedersen 1992, 1993). The effect of the early visual experience with the farm environment was studied by Pedersen (1991). Pedersen either opened the solid wall of the nest boxes when the cubs were two weeks old and kept the boxes open from this time onwards or she did not open the boxes. When the cubs were tested at the ages of 14 and 28 weeks, the cubs with an open nest box had reduced fear reactions towards humans compared to the cubs that had been in the closed nest box. Similarly, Fox (1972) hand-reared wild canids and found that also wild red foxes may become attached to humans if taken under human care during their primary socialisation period (Fox 1972; Belyaev et al 1985). During the next years, the foxes' primary social attachment to Fox remained permanent and they showed submissive greetings and play solicitation towards him. However, unlike more social wild canids, red foxes tended to avoid physical contact with humans and were at an earlier age wary of strangers, demonstrating the limited capacity of the red fox to develop secondary social relationships.

Whether or not there are sufficient amounts of human contacts to assure primary socialisation to humans, farmed animals may still later in their lives suffer from too few human contacts. According to the evolutionary approach, the feralisation process is considered as the reverse of domestication, requiring genetic changes at the population level (Price 1999), and thus not being possible to happen during one generation. However, a more ontogenetic approach suggests that an animal may become feral, as determined by behavioural criteria and by human-animal relationships, during its lifetime if it is never socialised to or is desocialised from humans (Daniels and Bekoff 1989). Examples given by Daniels (1988) are abandoned and stray dogs, i.e. dogs that are not receiving regular human care. Daniels (1988) found that these dogs avoided people and turned into feral dogs during their lifetime.

In farmed foxes, the amount and efficiency of human contacts may be affected by either the quantity or quality of living conditions (Bakken et al 1994). Pedersen and Jeppesen (1998) found that increasing cage size from 1.2 to 9.6 m^2 increased singly housed silver foxes' fear reactions towards humans. Similarly, blue foxes housed singly in a smaller area (0.8 m^2) were less afraid of humans than foxes housed in a larger area (2.5 m^2) (Korhonen et al 2000). Furnishing cages with either nest boxes or resting platforms has reduced (Jeppesen and Pedersen 1991, 1992), increased (Pedersen et al 2002) or has had no definite effects on the fearfulness of the foxes (Harri et al 1995; Korhonen and Niemelä 1996c) (see Mononen 1996, Rekilä 1999).

Another way to increase an animal's social attachment to humans is to select animals for confident behaviour (Belyaev et al 1985; Rekilä et al 1997, 1999) which is a trait with a high heritability (Belyaev et al 1985; Nikula and Kenttämies 1997). Creating positive relations between farmed foxes and humans could be a feasible and beneficial way to promote the welfare of foxes. The beneficial effect of a hereditary confident behaviour on physiological welfare has already been demonstrated by Rekilä et al (1999). Farmed silver foxes that had a lower level of fear towards humans (measured by the feeding test scores) had lower cortisol levels after adrenocorticotrophic hormone (ACTH) administration than the foxes that were more afraid of humans.

2.4.4 Summary

Farm animals seem to deal best with the species-specific group sizes and compositions. Since the basis of the behaviour of the domesticated species is founded on the behaviour of the species' wild ancestors, natural behaviour should be taken into account when designing housing systems for the farmed animals. Both the group size and the composition of the group *should be adjusted carefully for the species. Suitable group composition helps the animals to form a stable social system within the group and makes aggressiveness less necessary. The quality of space seems to be a more crucial factor for the farmed animals than the quantity per se. For group-housed animals, space must be guaranteed for exercise and movement as well as for interaction or avoidance of interaction with their group members and with humans. Fear of humans in farmed animals can be reduced either by early handling or by selecting animals for confident behaviour. Furthermore, close human contacts should be guaranteed throughout the animals' lifespan in order to avert desocialisation of animals.*

3 AIMS OF THE STUDY

The traditional silver fox farming practice includes that fox cubs are weaned from their mother at the age of approximately eight weeks. Thereafter, the cubs are kept either singly or in sibling pairs, most often in male-female pairs, in fox cages (115 x 105 x 70 cm, L x W x H). This way of housing farmed foxes has been impugned due to foxes' possibly limited chance to exercise and to show social behaviour. Therefore, the premise of the present study was to introduce alternative feasible housing systems for farmed foxes.

Compared to the traditional housing practice, the alternative housing systems introduced in the present study included changes either in the foxes' social environment or in their physical environment or both. The effect of the social environment was assessed by either including or excluding the vixen into or from the groups as well as by changing the number of foxes within the housing systems. Spatial requirements were studied by allocating different amounts of space to foxes as well as by changing the quality aspects of the living area. In designing these new housing systems, both the practicality and the species' social and spatial behaviour in the wild were taken into account.

The hypothesis underlying the experimental design was that if the living conditions in traditional housing systems are limiting foxes' species-specific social behaviour and locomotor behaviour then in the more diverse social and physical environment, the foxes' welfare presumably would be enhanced. Therefore, the aim of the present study was to establish the welfare effects of the different housing conditions by comparing measurable behavioural, physiological and production-related welfare indicators in farmed silver foxes housed either in the traditional fashion or in the presented alternative housing systems during their growing seasons (June-January). Furthermore, the impact of various housing conditions on human-animal relations was determined. In defining the causative factors for the possible welfare effects, the knowledge of the behaviour of the wild red fox was exploited.

4 MATERIAL AND METHODS

The materials and methods used in the original papers of this thesis (I-IV) are summarised below. A more detailed description of the materials and methods used can be found in the original papers. A summary of the social and physical systems explored and the methods used in studies I-IV are presented in Tables 1 and 2, respectively. The present study also contains previously unpublished data. Unpublished data is based on the studies presented in the original papers and marked with superscript [u].

4.1 Animals and housing conditions

The experiments were carried out over the years 1996 and 1998-2000 and performed during the growing seasons, i.e. from June-July until the cubs were pelted in January. The silver foxes used were born in traditional fox cages (115 x 105 x 70 cm, L x W x H, Fig. 1). The experiments included both silver fox vixens and their cubs (I, II) or cubs exclusively (III, IV). Cubs of both sexes were used in all experiments.

Figure 1. Silver fox in a traditional fox cage.

In the experiments where all the silver foxes were housed in shed houses, the foxes were divided into their experimental groups after reaching the age of eight weeks (I, IV). In II and III, where foxes were housed either in enclosures or in cages, the foxes were transferred from the cage environment to the enclosures at the time when the cubs were either eight weeks (II) or approximately 16 weeks (III) old. In these studies, the cubs that were housed singly in cages were separated from their mother at the age of eight weeks, kept in sibling groups until the age of 10-14 weeks (II) and approximately 16 weeks (III) and housed thereafter singly.

Table 1. The summary of the social and physical systems used in I-IV. C = cage, E = enclosure.

	I	II		III		IV		
Housing type	C	C	E	C	E	C	C	C
Group size [a]	6	1	5	1	4	1	2	4
Number of housing units	4	58	6	24	6	14	14	14
Total number of cubs	20	48	24	24	24	14	28	56
Total number of vixens	4	10	6					
Space per animal, m^2	1.2	1.2	10/22.5	1.2	12.5/28.1	1.2	0.6/1.2	0.6/1.2
Total space, m^2	7.2	1.2	50/112.5	1.2	50/112.5	1.2	1.2/2.4	2.4/4.8

[a] group size = number of foxes per housing unit

In the shed houses, the foxes were housed either in family units consisting of a vixen and five of her cubs (I) or singly (vixens in II, cubs in II, III and IV), in male-female pairs of cubs (IV) or in quartets consisting of two male and two female siblings (IV). When a vixen and her five cubs were housed together, the housing system was constructed out of six traditional cages connected together by openings (20 x 20 cm, L x H) through the walls between the adjacent cages (shared cage system, see Fig. 1 in I). The space for the whole group and per individual was, therefore, 7.2 and 1.2 m^2, respectively (I). The singly housed foxes (II, III, IV) were always housed in a traditional fox cage. The housing systems for the cubs housed in pairs and in quartets were made up of one or two and two or four traditional cages, respectively (IV). Space allocation (i.e. the amount of space per individual animal) for pair and quartet housed cubs was, therefore, either 0.6 or 1.2 m^2 per individual (IV).

In the enclosures, two male and two female siblings were housed either with (II) or without (III) their mother. The enclosures, fenced with 2-m high wire mesh, were built on solid ground (Fig. 2). Two of the enclosures measured 5 x 10 m (L x W), four 7.5 x 15 m. Natural vegetation with grass and occasional trees as well as stones were left in the enclosures. In each enclosure, there were one (II) or two (III) nest boxes and a resting shed (Fig. 2). The space allocation for individual foxes housed in the enclosures varied between 10.0 and 22.5 m^2 (II) or between 12.5 and 28.1 m^2 (III).

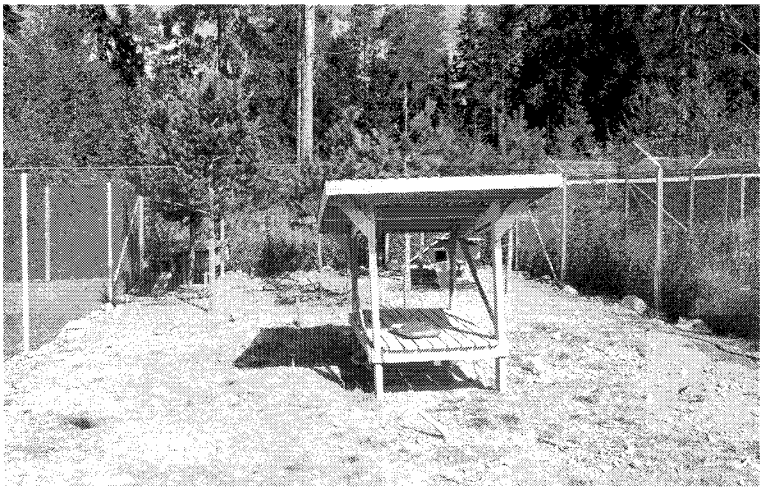

Figure 2. One of the experimental enclosures (112.5 m^2) with constructions built up for foxes.

4.2 Behavioural measurements

The behaviour of the foxes was monitored either by direct visual observations (I, II, III) or by video-recordings (II, III, IV). The time spent in active behaviours (sitting, standing, moving) and passive behaviours (sleeping or lying awake) was determined for 24-h days (III, IV) or during the daylight hours (I, II).

For the foxes housed in the enclosures, the use of the nest boxes and the resting shed was determined (II). For the foxes housed in the cage environment, the use of different cages (I, IV) as well as the use of resting platforms, group preference index (GPI) (Gattermann 1990) and locomotor stereotyped behaviour (IV) were monitored. GPI presented here is a comparative value of a preference for staying in groups computed from the paired relations occurring in a group (Gattermann 1990). The time (% of total time) spent in singly performed locomotor stereotypies was analysed from the December video-recordings (IV). Only locomotor stereotyped behaviour, i.e. repeated pacing or jumping along the cage wall without any obvious goal or function (Fraser and Broom 1990; Broom and Johnson 1993; Mason 1991, 1993) and performed without the neighbour, was monitored in the present study.

The feeding test, performed according to Rekilä et al (1997), was performed for the foxes in mid-August, late August, late September, late October and late November (IV). The feeding test categorizes animals according to their attitude towards humans: animals that will eat in the test are considered as less fearful and more confident towards humans than those animals that will not eat in the test.

Table 2. The summary of the methods used in I-IV. GPI = group preference index, ACTH = adrenocorticotrophic hormone, C-C = cortisol-creatinine, SIH = stress-induced hyperthermia, GAST = gastrocnemius muscle, SDH = succinate-dehydrogenase activity.

	Studies	References
Behaviour		
Activity	I[a], II, III, IV	e.g. Harri et al 1999; Korhonen et al 1999; 2001d
Stereotypies	IV	e.g. Jeselnik and Brisbin 1980; Wikman et al 1999; Korhonen et al 2001a, d
Use of platforms	IV	e.g. Mononen 1996; Mononen et al 1997
Feeding test	IV	e.g. Rekilä et al 1997; Rekilä et al 1999
GPI	IV	e.g. Gattermann 1990
Physiology		
Body mass at pelting	II[u], III[u], IV	e.g. Broom and Johnson 1993
Adrenal mass	II, III, IV	e.g. Selye 1950; Gómez et al 1996; Hemsworth et al 1996
ACTH-test	II, III, IV	e.g. Fraser and Broom 1990; Terlouw et al 1997
Urinary C-C ratio	IV	e.g. Lasley and Kirkpatric 1991; Beerda et al 1999b; Rekilä et al 1999
SIH	II, III, IV	e.g. Moe 1996; Moe and Bakken 1997a, b; Korhonen et al 2001c
Mass of heart	II, III[u], IV	e.g. Harri et al 1982; Duncan et al 1998
Mass of GAST	II, III[u], IV	e.g. Duncan et al 1998
SDH in GAST	II, IV	e.g. Pennington 1961; Harri et al 1982
Breaking force of tibia	II, IV	e.g. Korhonen et al 2000, 2001c
Production		
Bite wounds	III, IV	e.g. Bakken et al 1994
Quality of furs	II[u], III[u], IV	e.g. Krzywiecki et al 1996; Korhonen et al 2000, 2001c

[a] including measure of the use of available space, aggressive acts, synchrony of activity, [u] unpublished data

4.3 Physiological and production-related measurements

Body mass of the animals (II[u], III[u], IV) and incidence of bite wounds from the leather side of the skins (III, IV) were determined at the pelting time. Professional fur graders at the Finnish Fur Sales Ltd (Helsinki, Finland) evaluated the quality of furs using a 10-point scale (1: poorest, 10: best) (II[u], III[u], IV).

Stress-induced hyperthermia (SIH) test was performed in October-November (II, III, IV). The SIH test is based on the idea that an animal's acute reaction to human's presence can be interpreted from changes in the animal's rectal temperatures (Moe 1996) and the presence of the human causes SIH (Bakken et al 1999). Therefore, SIH can be used as a measure of the animals' responses to human handling and restraint in farmed silver foxes (Moe and Bakken 1997a).

The increased hypothalamic-pituitary-adrenal (HPA) axis activity of the animals, indicating the negative emotional reaction of the animals (Mason 1968) to the social and physical housing conditions was determined via the urinary cortisol-creatinine (C-C) ratio in October (IV) as well as by determining the serum cortisol level two hours after ACTH administration (II, III, IV) and the mass of adrenals at the pelting time (II, III, IV). Urinary C-C ratio, as a non-invasive method to measure cortisol levels (Beerda et al 1996, 1999b), was used in order to avoid problems related to blood sampling procedure (Fraser and Broom 1990; see European Commission 2001). Long-term effects of the housing systems on the welfare of the foxes were further assessed by the ACTH-test. Although chronic stress may not generally be measured by changes in the HPA-axis activity due to efficient feedback mechanisms in this system, chronic stress can affect the responsiveness of the adrenal cortex (Terlouw et al 1997). The ACTH-test is based on the idea that an animal that uses its adrenal cortex frequently is likely to have more active cortical enzymes than an animal that has to rely on its adrenal cortex less often (Fraser and Broom 1990; Broom and Johnson 1993). Therefore, an injection of a large dose of ACTH will evoke a higher serum cortisol level in those animals that have been under more stress. Although there is some divergence in the interpretation of the results obtained in the ACTH challenge test (see Rushen 1991), many research reports support the view that the increased response to ACTH can be used as a measure of long-term stress (see Fraser and Broom 1990; Broom and Johnson 1993; Terlouw et al 1997) in several animal species including farmed silver foxes (Rekilä et al 1999), and that it is a more valid measure and less subject to errors than a baseline cortisol assay. Long-term stress may, further, induce adrenal hypertrophy (Selye 1950; Gómez et al 1996; Hemsworth et al 1996).

It is hypothesized that in larger housing systems, animals have a greater possibility to exercise. This exercise is likely to change some exercise-related indices (e.g. Harri et al 1982, 1984; Duncan et al 1998). Therefore, the masses of heart and gastrocnemius muscle (GAST) (II, III[u], IV) as well as the succinate-dehydrogenase (SDH) -activity of the GAST and the breaking force of the left tibia were measured (II, IV).

5 RESULTS

The results from I are based on the behavioural data from the whole families, in contrast to other experiments (II-IV) which contain behavioural and physiological results from individual animals. Therefore, the behavioural events from the family housing experiment performed in cage conditions (I) are presented separately from the other results. A brief summary of the results obtained from the cubs in experiments II-IV is presented in Table 3. Since the environment in the enclosures was very different from the more controllable cage environment, the results from the experiments including housing of foxes in the enclosures are expressed as an entity (II, III). With regard to the results from IV, no significant interactions between the examined group sizes and space allocations were found and only the main effects of these factors are presented. With regard to all results, only statistically significant differences ($p<0.05$) have been considered as true differences.

5.1 Mortality and morbidity

The number of foxes injured, falling ill or dying during the present experiments remained fairly low. In the cage conditions, two female cubs from the family with the earliest aggressive acts were found injured in late September and had to be taken out of their family unit (I). From the cubs housed singly, one male and one female cub were found dead in late November and in mid-October, respectively (IV). The reason for the death of these cubs remained unknown. From the siblings housed in quartets in cage conditions, one male in a four-cage system was removed from its group in late October due to an ear mite infection (IV). From the sibling groups housed in the enclosures, two female cubs were found dead in one enclosure (III). One female was fatally injured to its jaw in mid-October, the other died because of an intestinal disorder in mid-December. Accordingly, it seems (there were too few cases to run statistics) that mortality and morbidity were not connected to any special housing system.

5.2 Families in the cage environment

In the families consisting of a vixen and her five cubs, the time spent in active behaviours within families increased significantly from July-September (16-23 %) to October (36-48 %)

(I). Furthermore, the synchrony of activity decreased with advancing time, i.e. the number of individuals resting or being active together within families became more randomised (I).

The use of available space changed as the cubs grew older (I). In early July, the individuals within families were distributed most often into 1-4 cages and only occasionally five or six cages were simultaneously occupied. However, from August onwards, generally 3-4 cages were occupied and, with the advance of autumn, situations where there were all cages occupied became more frequent.

The first distinct acts of aggressions between family members were observed in late August when the cubs were about 15 weeks old (I). Thereafter, the number of aggressive acts during observation sessions increased even though aggressiveness was rather rarely observed. Aggressiveness between the group members was most common at the end of the experiment in late October, the cubs being approximately 23 weeks old.

5.3 Seminatural enclosures versus traditional cages

5.3.1 Vixens

Vixens were housed either with their four cubs in large enclosures or singly in traditional cages in shed houses (II). Different housing systems had no effects on vixens body mass, the HPA-axis activity, the emergence of SIH or the exercise-related parameters, except on the SDH-activity of the GAST which was higher in these vixens housed in the enclosures (II).

5.3.2 Cubs

The time spent in active behaviours during the light hours was higher in the cubs that were housed in cages (II, III) but the total time of the 24-h day spent in active behaviours was greater in the cubs housed in the enclosures (III). Furthermore, the activity rhythm, especially in late autumn, was different between the cubs housed in the enclosures and in cages (III). In the foxes housed in cages, the main activity occurred during the working hours (0800-1600 h) whereas the foxes housed in the enclosures were most active during the evening hours (1600-0000 h).

For the cubs housed in the enclosures, the time spent in the nest box decreased with advancing autumn (II). The cubs preferred more and more to use the roof of the resting shed that was 115-165 cm above the ground level.

Table 3. The summary of the results obtained from the cubs in II-IV. SA = space allocation (0.6, 1.2 m^2), GS = group size (1, 2, 4). GPI = group preference index, ACTH = adrenocorticotrophic hormone, C-C = urinary cortisol-creatinine, SIH = stress-induced hyperthermia, GAST = gastrocnemius muscle, SDH = succinate-dehydrogenase activity. C = cage, E = enclosure. NS = non-significant, p>0.05. - = not analysed.

	II with vixen	**III** without vixen	**IV** without vixen	
			SA	GS
Behaviour				
Activity	light hour activity: C>E	C<E, C: peak 0800-1600 h, E: peak 1600-0000 h	NS	0800-1600 h: 1>(2, 4)
Stereotypies	-	-	NS	1>(2, 4)
Use of platforms	-	-	0.6<1.2	1<2<4
Feeding test, number of eaters	-	-	NS	1>2>4
GPI	-	-	pairs: NS quartets: 0.6>1.2	pairs: NS quartets: Aug>Dec
Physiology				
Body mass	♂: C>E,♀: C=E [u]	C>E [u]	NS	NS
Adrenal mass	C<E	NS	NS	NS
ACTH-test	C<E	NS	NS	NS
Urinary C-C ratio	-	-	NS	NS
SIH	C<E	C<E	NS	NS
Mass of heart	C<E	C<E [u]	0.6<1.2	NS
Mass of GAST	C<E	C<E [u]	NS	NS
SDH in GAST	C<E	-	NS	NS
Breaking force of tibia	C<E	-	NS	NS
Production				
Bite wounds	-	C<E	in males: NS in females: 0.6>1.2	NS
Quality of furs	NS [u]	C>E [u]	0.6<1.2	1>2>4

[u] unpublished data

In the SIH test, the time needed to catch the cub from its home environment did not differ between the cubs housed in the enclosures and in cages (II, III). This was possibly due to the fact that most of the cubs in the enclosures fled into their nest boxes when humans entered their enclosure and were, therefore, easy to catch. The rectal temperature measured at the beginning of the SIH test was lower in the cubs housed in the enclosures than in cages (II) or was not affected by the housing system (III). However, the rectal temperature measured 35 min after human exposure and restraint as well as the change in the temperature between the two measures was higher in those cubs that lived in the enclosures (II, III).

Silver fox cubs that were housed in outdoor enclosures with their mother had heavier adrenals as well as a higher serum cortisol level two hours after ACTH administration than the cubs housed singly in a traditional fox cage in outdoor shed houses (II). However, when the mother of the cubs was omitted from the group, no significant difference was observed in the HPA-axis activity between the cubs housed in sibling groups in the enclosures and singly in cages (III).

The mass of heart (II, III^u: Table 4, sex NS, group $p<0.05$, ANCOVA with dry skin length as a covariate), the mass of GAST (II, III^u: Table 4, sex NS, group $p<0.01$, ANCOVA with dry skin length as a covariate), the SDH-activity in the GAST and breaking force of tibia (II) were greater in the cubs that were housed in the enclosures than in cages. However, the body mass was predominantly lower in the cubs housed in the enclosures than in the cubs housed singly in cages (II^u: Table 4, for males: $p<0.05$, for females: NS, Mann-Whitney test; III^u: Table 4, sex $p<0.001$, group $p<0.01$, ANOVA).

Table 4. Body mass (kg), mass of heart and gastrocnemius muscle (GAST) (g) and quality of furs (a 10-point scale, 1: poorest, 10: best) in the silver fox cubs housed either in the enclosures (E) or in cages (C). Results are based on the studies II and III. All results are expressed as mean±SD. See text for statistics. M = male, F = female. Shaded area: previously unpublished data.

	II				**III**			
	C		**E**		**C**		**E**	
	M	F	M	F	M	F	M	F
Body mass, kg	8.2±1.2	6.8±0.9	7.3±0.6	6.6±0.7	8.2±0.8	6.8±0.9	7.3±0.8	6.3±0.6
Heart, g	46±5	40±3	48±4	41±5	46±6	40±5	48±6	42±4
GAST, g	34±4	29±3	36±3	32±3	33±3	30±3	35±4	30±3
Quality of furs	8.2±0.7		7.7±1.4		7.1±0.8		6.1±1.4	

The number of bite scars in the leather side of the fleshed skins was higher in the cubs housed in the enclosures as sibling groups than in the singly cage housed cubs (III). The quality of the furs was either not affected by the housing environment (II^u: Table 3, $p>0.1$, Mann-Whitney test) or was worse in the foxes housed in the soil floored enclosures (III^u: Table 3, $p<0.01$, Mann-Whitney test).

5.4 Group size and space allocation in the cage environment

In general, the singly housed silver fox cubs spent more time in active behaviours during the working hours (0800-1600 h) and, on the other hand, were resting more during the early hours (0000-0800 h) than the cubs housed either in pairs or in quartets (IV). Furthermore, these singly housed cubs spent more time in locomotor stereotyped behaviours during the 24-h day in December than the other cubs (IV). Available space per individual had no significant effects on the activity level or on the incidence of locomotor stereotyped behaviours.

The cubs housed in pairs in the double-cage system and in quartets either in the double-cage or in the four-cage system all preferred the first cage (in the double-cage systems) or the first two cages (in the four-cage systems) nearest to the door by which humans normally entered the shed house to the cages situated in the rear parts of the cage system (IV). Space allocation (0.6 or 1.2 m^2 per individual) did not affect the preference for using any particular cage. In general, the use of the resting platforms decreased with time (IV). The use of platforms increased with increasing group size and space allocation.

In the pair housed cubs, the GPI did not change with the advance of autumn but in the quartets, the GPI decreased from August till December (IV). Space allocation had no effect on the GPI in the pair housed cubs. In quartets, the GPI was significantly lower in those cubs that were given a larger space allocation.

The percentage of animals that never ate during the five feeding tests performed during the growing season was highest in those foxes housed in quartets (IV). From the five separate feeding tests, only the test performed in late October revealed in a significant manner this difference between the different group sizes. Space allocation did not affect the percentage of animals coming to eat during the feeding tests.

Neither the group size nor the space allocation affected the C-C ratio and SIH in October, the serum cortisol level after ACTH administration and the adrenal mass at the pelting time in January (IV).

The heart tended to be lighter in the quartet housed cubs than in those cubs housed either in pairs or singly (p=0.065) (IV). The cubs that were housed with larger space allocation (1.2 m^2) had heavier hearts than the cubs housed at 0.6 m^2 per individual. Neither the group size nor the space allocation affected the body mass of the cubs (IV). No significant differences in the mass of GAST, the SDH-activity of the GAST or in the force needed to break the tibia emerged either by examined group sizes or space allocations (IV).

In general, male cubs had better fur quality than females (IV). The quality of the furs decreased with increasing group size and with decreasing space allocation. Group size had no effects on the incidence of bite wounds (IV). A larger space allocation decreased the number of bite wounds in the female cubs but no differences were found in the male cubs.

6 DISCUSSION

The aim of the present study was to evaluate the effects of different social and spatial housing systems on physiological, behavioural and production-related welfare parameters in farmed juvenile silver foxes. The main emphasis was placed on the juveniles because approximately three-quarters of all farmed foxes are pelted before they reach maturity. Spatial requirements were studied by changing the quality and the quantity of the animals' living area. The effects of social conditions were assessed by changing group composition and group size. In evaluating the suitability of different housing conditions for farmed foxes and the compatibility of the adaptations possessed by the foxes with the challenges posed by the housing environment in which they live, the knowledge of the behaviour of the wild red fox was exploited. The experimental groups always comprised of foxes related to each other but the compositions of the groups were, however, standardized by sex by removing extra cubs from the groups (except in I). The situation that each fox family on a farm should consist of e.g. two male and two female cubs is highly improbable. Due to the standardization of the groups, it is worth emphasising that the final applicability of the present results into practice has to be assessed in future field experiments.

6.1 Social environment

In cage conditions, the most distinguishable behavioural result obtained with regard to group size was that those cubs weaned straight into single living at the age of eight weeks spent significantly more time in singly performed locomotor stereotyped behaviours in December (almost 4 % of a 24-h day) than the cubs weaned into sibling pairs or quartets (less than 1 %) (IV). Wikman et al (1999) reported that singly housed silver fox cubs - not weaned straight into single living - at the age of 3-4 months performed locomotor stereotypies without the neighbouring animal during 0.3 % (median 0.7) of a 24-h day. In 1-4 years old silver foxes, the corresponding number was 0.3 % (3.2) (Kasanen et al 2001). Although stereotyped behaviour develops with time (Mason 1991, 1993) the cubs weaned straight into single living in the present study spent at the age of 7-8 months even more time in stereotyped behaviour than the adult silver foxes who were not weaned directly into single living.

Increased stereotyped behaviour may have been induced by separate housing throughout the growing season, as has been previously noted in kennel, zoo and laboratory animals (Hetts et al 1992; Hubrecht et al 1992; see Dantzer and Mittleman 1993; Beerda et al 1999a). On the other hand, increased stereotyped behaviour in the singly housed cubs in December may be due to their past experience (see Dawkins 1998) of being separated from their families at an early age as such. In the wild, the age when red fox cubs become independent is approximately 6-8 months (Gittleman 1989; Nimon and Broom 2001), i.e. the cubs may stay with their families much longer than the eight weeks used in the present study. Furthermore, the siblings are strongly bonded to each other (Scott 1967) and even at the time of dispersal, siblings tend to migrate in the same direction (Harris and Trewhella 1988; Allen and Sargeant 1993). Hence, the incompatibility of the foxes' adaptation for staying in family groups longer than eight weeks with the social challenge including early separation resulted in the cubs expressing a higher amount of locomotor stereotypies.

Although the isolated cubs may have experienced some welfare problems, no differences in the HPA-axis activity between either the singly, pair or quartet housed cubs were revealed (IV). The reason for this may be that there really is no clear and established correlation between the occurrence of stereotypies and physiological stress parameters (Ödberg 1989; Dantzer and Mittleman 1993; Ladewig et al 1993). In some experiments, increased stereotyped behaviour has been negatively correlated to adrenocortical activity, in others a positive correlation has been found (see Ladewig et al 1993). Furthermore, although the individuals that exhibit stereotyped behaviour have difficulties in coping with their living environment (Fraser and Broom 1990; Broom and Johnson 1993), the exact role of stereotypies in helping an individual animal to cope has yet not been clarified (see Bildsøe et al 1990; Broom and Johnson 1993). Nonetheless, stereotypies may be regarded as indicators of long-term stress induced by management systems (Bildsøe et al 1990; Broom and Johnson 1993) and as a sign of problems in compatibility of adaptations with environmental challenges (Fraser et al 1997). In addition to increased stereotyped behaviour, the lack of conspecifics resulted in the higher activity level of the singly housed foxes during the working hours (0800-1600 h) and in the high number of animals coming to eat during the feeding tests (IV). This may indicate that the singly housed foxes were possibly seeking some kind of stimulus from the human activity occurring outside their cage. Therefore, it can be concluded that putting foxes directly into single living may jeopardize the welfare of these animals.

Thus, the companionship of conspecifics may alleviate the separation stress during and after weaning time, as well as acting as a social environmental enrichment for silver fox cubs.

However, despite the fact that silver foxes may gain psychological benefit from being kept with their siblings during the first months of their lives, the situation may be somewhat different after the onset of the natural dispersal time, i.e. from September onwards (e.g. Lloyd 1975; Allen and Sargeant 1993). With the advance of autumn, aggressiveness within the groups increased and the foxes tended to avoid each other, by decreasing the synchrony of their activity and by each using a separate cage in the six-cage housing system (I). Furthermore, the GPIs show that in groups of four silver fox cubs, the individuals within a group were more and more separated from each other with the advance of autumn, especially when the foxes were housed in a larger cage system (IV).

The tendency to avoid each other during the autumn was noticeable also during the feeding tests: in general, but especially in October, the percentage of animals coming to eat was lower in the quartets than in the singly or pair housed cubs (IV). The feeding test is validated to measure fear responses towards humans (Rekilä et al 1997). Therefore, the present result suggests that the cubs in quartets, housed in either two or four cage systems, were experiencing human proximity as more aversive than the other foxes. This may partly be the case since a large number of those foxes housed in larger cage areas fled to the far end of their cage system whenever humans entered their shed house. However, the SIH test did not reveal any differences in responses to human proximity and restraint between the foxes housed singly, in pairs and in quartets (IV). Therefore, in the present study, the feeding test might also indicate the effects of group housing and of social tension within each housing unit on the behaviour of the foxes rather than only the level of fear of humans (IV), as was also the case in a study where blue foxes were housed in sibling groups (Ahola et al 2002). This result, together with the findings that the social environment may influence the responses of farm animals to their environment (see Nicol 1995) and affect the individual stress responses to fear-eliciting situations (Grignard et al 2000), is further evidence that simple extrapolation from the behavioural or physiological observations gathered from singly or pair housed animals may not as such be applied to group-housed animals.

No differences in the HPA-axis activity were revealed between the cubs housed in sibling groups without their mother in the enclosures (III) or in cages (IV) and singly in cages. However, when the vixen was included into the family group in the enclosures, the increased HPA-axis activity of her cubs indicated that the cubs experienced more long-term stress than the cubs housed singly in traditional cages (II). Even when comparing the results between II and III, the highest serum cortisol levels after ACTH administration and the heaviest adrenals were detected in the male cubs housed with their mother. In cage conditions, increased aggressiveness may have been a sign of the negative effect of the mother on the whole group (I). These results show that although the presence of conspecifics may be one of the most powerful ways to enrich animals' living conditions (Mendl and Newberry 1997), an inappropriate group composition may transform this positive effect into a negative factor.

The reason for the increased aggressiveness and increased adrenocortical activity in the cubs housed with their mother may be a sign of a parent-offspring conflict, presented by Trivers (1974). According to Trivers (1974), there will arise a mismatch between the parents and their offspring in their willingness to contribute (parents) and to obtain (offspring) care. The young want to receive care from their parents more and for longer periods than the parents are ready to give. The parents' unwillingness to give all the care that their young demand is due to their own need to balance their resources (e.g. body's energy stores) so that these resources are not totally exhausted in the care-taking of the present young but that a portion is saved up also for the next years' offspring. Although the conflict between the parents and the young is most pronounced at weaning (Trivers 1974; see Manning and Dawkins 1998) and most probably should influence both the parents and the young, in the present experiment this conflict may have had long-term effects only on the fox cubs.

The other explanation for the impaired welfare of the cubs housed with their mother may be the dispersal behaviour of the species under natural conditions. In the wild, when red fox cubs are approximately four months old, the parents start to ignore them or even become hostile towards them (Zimen 1984; see European Commission 2001). Eventually, after having reached their independence at the age of 6-8 months (see Gittleman 1989; Nimon and Broom 2001) cubs leave their natal home range, with the main dispersal time occurring during September-December (e.g. Lloyd 1975; Storm and Montgomery 1975; Allen and Sargeant 1993). Although Harris and Smith (1987) found that social groups of red foxes may contain also surplus males, usually male pups leave their natal territory first and travel further (e.g. Hersteinsson and Macdonald 1982; Harris and Trewhella 1988). Female cubs may stay in their natal territory with their mother (e.g. von Schantz 1981; Hersteinsson and Macdonald 1982; Macdonald 1983). Accordingly, when the adaptation for dispersal behaviour was prevented in the present study, the cubs, especially the male cubs, were possibly experiencing stress due to the increased within-group social tension (Fig. 3, II).

Figure 3. A vixen with an aggressive gape directed towards its male offspring in late September.

The cubs housed in groups without their mother fared better than the ones with their mother (II, III) possibly also due to differences in the strength of the bonds between different aged individuals (Scott 1967). The period of intense maternal care begins to wane when the cubs are 2-3 weeks old (Scott 1967). Therefore, even during the period of socialisation, the young cubs are more and more in one another's company while the mother leaves her pups for long periods to prey for food for her young. Hence, the bonds are apparently more intense between the littermates than between the mother and her cubs because the time spent in mother-offspring interaction is far less than the proportion of time in interactions between littermates. The tendency of the fox littermates to disperse in the same direction (e.g. Allen and Sargeant 1993) further supports this idea. Similarly, farmed blue foxes of the same age tend to have more social contacts with each other than the animals of different ages (Korhonen and Alasuutari 1995).

Different social and physical environments did not affect the physiological indices of the mothers (II). This is in agreement with previous reports of blue fox vixens housed with their cubs (Ahola et al 2000). The reason for this finding may be that the vixens had already lived through group, pair and solitary lives before the experiments. This simply shows that ontogeny of an animal impinges on its later physiological and behavioural capabilities (e.g. Mononen 1996; Fraser et al 1997).

Bakken et al (1994) reported a study in which silver foxes were housed either singly or in groups consisting of two, four or eight cubs of unknown relationship and of unknown sex. In the larger groups, there were some problems with biting damage although the quality of furs was not affected by the group sizes. Krzywiecki et al (1996) observed that housing foxes either singly or in threes had no effects on the quality of their furs. In the present study, the presence of littermates did not increase the incidence of bite wounds in individual foxes in cage conditions (IV). However, the decreased quality of furs (III^{u}, IV) and the increased incidence of biting wounds (III) in the group-housed foxes in the enclosures indicate either an increased incidence of fights leading to bitings or of play behaviour which also may result in biting damages (see IV). In the wild, the social order within the litter of fox cubs forms already during the first five weeks of their lives (Henry 1986). Thereafter the level of aggression between the cubs declines with the developed social hierarchy. The bite scars found in the singly housed foxes may have arisen at the time when they were still with their siblings (III). However, the number of wounds was significantly higher in the group-housed foxes in the enclosures than in the singly housed foxes (III). This indicates that aggressive acts occur also after the dominance hierarchy has been established for the first time. Furthermore, the number of aggressive acts between the group members during the autumn increased (I), and in quartets where there were only two feeding plates available the quality of furs was distinctively lower than in those housing systems where each animal had its own feeding plate (IV). These results suggest that the aggressive behaviour of the group members towards each other possibly is the source of the bite wounds. The present results on silver foxes, in conjunction with the earlier results on blue foxes (Korhonen and Alasuutari 1991, 1992), show that fighting during the feeding times may be one of the greatest reasons for aggressiveness between the group members of farmed foxes. Similarly, in the wild, the increased amount of food resources has been found to be the factor facilitating group living in the wild red fox (Macdonald 1983; von Schantz 1984). Accordingly, the aggressiveness between the individuals within a group leading to poorer fur quality and increased incidence of bite wounds may partly be alleviated by providing each fox within a group with a feeding place of its own.

Earlier studies in cage conditions have revealed that group-housed silver foxes are more active (Bakken et al 1994) and have better growth (Bakken et al 1994; Krzywiecki et al 1996) than singly housed foxes. In the present study, no differences in the body mass, or in the total daily activity, between the animals housed in different group sizes in the cage environment were recorded (IV). However, in the enclosures, the group-housed cubs were significantly lighter than those living singly in the cage environment at the pelting time (III[u]), possibly simply because of the increased activity of the foxes housed in the enclosures (III) (cf. blue foxes Korhonen et al 2001c). This increased activity may have been a consequence of either the increased possibility to exercise and patrol the area in large enclosures (III) or increased aggressiveness in the families leading to avoidance behaviour (I). That the synchrony of activity became more randomized with the advance of autumn (I) may indicate the onset of the natural dispersal time, and be a sign of a possible solitary nature of foxes (see Cavallini 1996), in contrast to more social animals which tend to synchronize their feeding activity and sleeping etc. (Nielsen 1999).

Despite possible problems due either to group size or to group composition, the foxes housed in groups may have gained some enrichmental value from their group mates. The foxes housed singly in cage conditions centred their highest activity around the hours when humans were active on farm (III, IV). This may be a sign that they were seeking social stimulus from the human presence in the absence of cage mates. Similarly, Korhonen and Niemelä (2000) found that singly housed farmed blue foxes sought stimulation from wooden gnawing blocks most during the hours between midnight and eight o'clock in the morning. Although group-housed foxes may have gained enrichment from their group mates, one still has to bear in mind that the changed activity rhythm may, in fact, be a sign of the feralisation of these animals (II, III; Daniels and Bekoff 1989). This feralisation, in turn, may compromise the welfare of the animals kept under human care (Rushen et al 1999).

6.2 Physical environment

Although it is often a source of criticism, the available space for the farmed foxes may not be the most crucial environmental challenge that faces the animals (Bakken et al 1994). Earlier studies have shown that neither decreasing the space into less than a half of a standard cage size (pair housed blue foxes: Korhonen et al 2001c) nor increasing the space by eight-fold (silver fox: Pedersen and Jeppesen 1998) has any radical impact on the welfare, measured by several physiological and behavioural parameters, of farmed foxes. On the other hand, with increasing cage size, locomotor stereotypy has been reported to increase in pair housed blue foxes (Korhonen et al 2001d).

In the present study, space allocation in the cage environment had no effects on the time spent in locomotor stereotypies (IV). Furthermore, it did not affect radically the measured physiological parameters. On the other hand, the cubs housed with their mother in large enclosures with excessive amount of environmental enrichment had a more active HPA-axis indicating that these cubs were experiencing more long-term stress than the singly housed cubs in the cage environment (II). These results reveal that the social housing environment had a greater influence on the welfare of the foxes than the quantity of the space. Not even the high amount of environmental enrichment in the enclosures could overcome the effects of the presence of the mother within the group (II). It seems that the social environment rather than the quantity of space could be one of the key features (see Harri et al 1996) in the foxes' environment which impacts on the welfare of the animals.

Figure 4. Silver fox cub on the roof of a resting shed.

The importance of the quality aspect of the living environment emerged also in the foxes' preference for certain constructions (II, IV). In both wild (e.g. Kolb 1986) and farmed foxes (e.g. Mononen et al 1996a; Harri et al 1999) some parts of the living area are more preferred than others. In the present study, the foxes housed in the enclosures spent almost 60 % of the observation time on the roof of their resting shed that was 115-165 cm above the ground (Fig. 4, II). The behavioural function for this adaptation of using elevated places may be the preference for an unobstructed view of the surroundings to achieve a better observation of approaching animals (e.g. prey, predators) and humans (wild foxes: Harris and Lloyd 1991; farmed foxes: Korhonen and Niemelä 1996b, c; Mononen et al 1996b, 1998a; Harri et al 2001).

In cage conditions, the foxes most often spent their time in the first one or two cages situated nearest to the door through which humans generally entered the shed house (IV). The same kind of behaviour has earlier been reported in laboratory dogs that did not utilize the extra space but preferred to stay in the front parts of their cages (Hite et al 1977). In silver foxes, the preference for the front parts of the cage area may be due to the general inquisitiveness of these animals towards human activity or the animals' tendency to ensure that there is some space available for escape from a sudden appearance of humans. Some areas were preferred to others, even though with larger group sizes GPI decreased (IV) and the number of available cages occupied simultaneously increased with the advance of autumn, the time of natural dispersal behaviour (I). It may be that when the tendency to avoid each other becomes more prevalent (Bekoff 1977), the subdominant individuals have to content themselves with less satisfying areas. The foxes' ability to choose between some more or less favourable areas may have promoted their sense of control which, in turn, is considered to be important for the welfare of animals (e.g. Fraser and Broom 1990; Broom & Johnson 1993; Webster 1995).

The extra space provided by the available platforms possibly enabled the quartet housed foxes to keep their own space even in only one or two cages out of four available cages (IV). Since resting platforms may act as extra space even for singly housed foxes (see Mononen 1996), the use of these constructions would be expected to increase as the space allocation gets smaller. However, in the present study the use of the platforms actually decreased with decreasing space allocation (IV). On the other hand, the quartet housed foxes spent more time on platforms than the singly or pair housed cubs (IV). Therefore, the present result shows that in group-housed foxes there may be other factors, different from those operating in singly housed foxes, controlling the preference for staying in platforms, and that the social environment can affect the animals' responses to their environment (Nicol 1995).

In the silver foxes housed in the enclosures, both the activity level and exercise-related physiological indices were higher than in those foxes housed singly in the cage environment (II, III[u]). As such, these results might be considered as positive for the welfare of the foxes, e.g. as an expression of freedom of movement (Gonyou 1996). However, this increased locomotor behaviour did not result in decreased stress as indicated by physiological stress-indices in the foxes housed in the enclosures (II, III). Only rather mild training programs have been reported to affect exercise-related physiological parameters (Harri et al 1982, 1984). Therefore, the higher exercise-related indices may have been simply due to different exercise profiles of the foxes (e.g. jumping on and off to the preferred roof of the resting shed) resulting more efficiently in changes in the muscle metabolism (cf. blue foxes Korhonen et al 2001c). This and the fact that in cage conditions the enlarged space available did not largely affect physiological and behavioural indices (IV), reveals that the exercise *per se* may be only a secondary need for foxes. In the wild, foxes have territories that have to be defended and patrolled to guarantee the food supply to the individual (e.g. Macdonald 1983). However, in farm conditions it may not be necessary to defend an area in order to assure food resources to the defender because sufficient food is available and foxes may have become accustomed to the stable, daily food supply. Therefore, it seems that the amount of space *per se* is not the most important environmental challenge (e.g. Stricklin 1995; Korhonen et al 2001a, c, d) and, as Grandin and Deesing (1998) suggest, limitation of movement may be less stressful to the animals than feed restriction.

In the sibling groups housed in the enclosures, the number of bite wounds per fox as well as the number of animals with bite wounds was higher than in the singly housed foxes (III). In cage conditions, space allocation did not affect the number of bite wounds in the male cubs whereas more bites were inflicted on the female cubs that were housed with the smaller space allocation (IV). The higher number of wounds in the foxes housed in the enclosures reveals that excessive space does not prevent the incidence of fur damage attributable to biting. Even in the wild as many as 7 % of foxes may die because of fights (Harris and Smith 1987). Furthermore, the quality of furs decreases (III[u]; blue fox: Korhonen et al 2000, 2001c) and the incidence of endoparasites increases, despite the conventional medication, in the foxes housed in soil floored housing systems (Reinisalo 2001). Therefore, the larger space with a soil floor may not be beneficial either to animals or to the fur farmers. In cage conditions, the deterioration of fur quality may have been a result of the crowded conditions (IV). The quality of furs decreased with increasing group size and with decreasing space allocation, i.e. the groups of four foxes housed in the area of 0.6 m^2 per fox were possibly suffering from a crowding effect (IV; Ahola et al 1996). The results obtained from cage conditions show that, at least from the producer's point of view, the combination of group size and space allocation must be carefully adjusted for the species.

6.3 Human-animal relations

The cage size or combination of size and furniture can allow animals such infrequent contact with humans that their fear towards humans increases (Pedersen and Jeppesen 1998) and they become almost feral (Bakken et al 1994). In the present study, the amount of space in cage conditions did not affect the foxes' reactions to human presence and restraint (the SIH test), although many of the foxes housed in cage systems comprising of several cages showed fleeing behaviour when humans entered their shed house (IV). However, the SIH test revealed that the foxes in the large enclosures sensed the proximity of human and restraint as more aversive and stressful than those foxes housed in cage conditions (II, III). In general, the SIH test is subjected to several confounding factors. The rectal temperature increases rapidly in stressful situations, possibly due to the fact that SIH may be related to the activation of the sympathetic-adrenal-medulla system (Moe and Bakken 1997a). The basal rectal temperature of silver foxes has observed to be 38.0-38.6°C (Moe and Bakken 1997a, b). However, in the present study, the mean rectal temperatures were already in the first measuring over 39°C. This suggest that the first temperature measured does not represent the basal temperature and that the use of radio telemetry would possibly have given more reliable results on the first temperature (cf. Bakken et al 1999). Furthermore, a part of the increased SIH in II and III may be due to the present experimental designs. Moving the foxes into a smaller SIH test cage may have affected more negatively the animals that had lived in large enclosures than the animals housed in traditional cages. Despite these concerns, the active avoidance of humans (e.g. during the SIH test) and the highest rectal temperatures after 35 min in the foxes housed in the enclosures indicated that the foxes in the enclosures perceived human proximity and restraint differently from the foxes housed in the cage environment (II, III).

Although the group size affected the activity rhythm of the cage housed foxes, this rhythm was, irrespective of the group size, in early winter typical of foxes housed in cage conditions, i.e. they had their highest activity during the working hours, 0800-1600 h (II, III, IV; e.g.

Mononen et al 1996a; Harri et al 1999). On the contrary, the daily activity rhythm of the foxes housed for months in the enclosures resembled the crepuscular activity rhythm of the wild foxes (II, III; e.g. Harris and Lloyd 1991). The change of temper in the foxes housed in the enclosures, indicating the feral nature of these animals (II, III; Daniels and Bekoff 1989), is quite explicable because the behaviour of domesticated farm animals still closely resembles that of their wild conspecifics (Mendl and Newberry 1997; see Rushen et al 1999).

In the case where silver fox cubs were housed without their mother, the fox cubs going through the feralisation process and experiencing human proximity as an aversive event were not suffering from long-term stress - at least not more than the foxes housed in traditional cage conditions (III). This may be due to the fact that they had, in the absence of their mother, some control over their environment and, hence, they were able to some extent to take effective action or to remove the threat (e.g. by fleeing from humans) (cf. Webster 1995). The finding that the foxes are not necessary suffering due to their feralisation *per se* is quite understandable. It may be that for an animal it is beneficial to be able to become feral during its lifetime in order to survive in the wild, e.g. in a situation where it has been abandoned or has escaped from human care and, therefore, has to be able to cope with living in the wild. However, the fact that the animals are experiencing human closeness negatively and, yet, are being kept under human care may cause a problem for the welfare of the animals and, furthermore, cause handling problems and increased incidence of injuries in both the animals and their human handlers (e.g. Rushen et al 1999).

Accordingly, on the one hand, the foxes housed in the enclosures had a better possibility to avoid daily human contact and, on the other hand, for humans it was more difficult to approach the animals. Due to these facts, the ontogenetic feralisation process accompanied with increased fear and avoidance of humans (Daniels 1988; Daniels and Bekoff 1989) became evident in the foxes housed in the enclosures (II, III). Not even the attempts to increase the habituation to humans by keeping the foxes for a longer period of time in cage conditions before the transfer into the enclosures prevented the feralisation of the foxes housed in large enclosures (III). Therefore, if farmed foxes are housed in large enclosures, there must be greater attempts to keep the foxes habituated to humans, e.g. by early handling of the animals (e.g. Pedersen 1991, 1992, 1993, 1994), by selecting the animals for confident behaviour (e.g. Belyaev et al 1985; Nikula and Kenttämies 1997; Rekilä et al 1997, 1999) or by reducing the animals' fear of humans by giving frequent positive rewards (Dale and Bakken 1992; Bakken et al 1993; Bakken 1998) (see European Commission 2001).

7 SUMMARY AND CONCLUSIONS

The present study demonstrates that the social and physical housing environment where foxes live in do affect the welfare status of juvenile farmed silver foxes. The results reveal that:

1. Social contacts are important and act as an environmental enrichment for young silver fox cubs. The significance of social companionship for young cubs is revealed by the findings that those cubs weaned straight into single living express locomotor stereotyped behaviour in December and seek social stimulus, in the absence of cage mates, from the human activity occurring outside their cage.

2. At the onset of the natural dispersal time, the presence of littermates, however, may compromise the welfare of some individuals. In the group-housed foxes, the increased aggressiveness and the high number of bite wounds as well as the tendency to avoid each other in the late autumn evidence that group housing of farmed silver foxes after the onset of the natural dispersal time (i.e. from September onwards) may not be beneficial for foxes.

3. The presence of a mother in a family housing system reduces the welfare of her cubs. The increased aggressiveness within the families and the higher HPA-axis activity in the cubs that were housed with their mother than in the cubs housed without their mother show that preventing the natural dispersal of the cubs from their mother's living area creates welfare problems, especially to male cubs.

4. The quality of the living environment is a more crucial factor than the quantity of the living space for farmed silver foxes. Roofs of the resting sheds in the enclosures and resting platforms in cages make the living areas of foxes more diverse, allow foxes to choose better their preferable places and provide foxes with an opportunity to observe their surroundings and to avoid other group members.

5. The quantity of living space provided to foxes influences the expression of human-animal relations. The active avoidance of humans, the higher SIH and the changed activity rhythm in the foxes housed in large enclosures demonstrate that an enlargement of the

living area elicits desocialisation of foxes from humans and results in, at least to some extent, feral-like foxes suffering from short-term stress in the proximity of humans.

6. Social and physical housing environment affects the quality of furs. A soil floor of the housing system worsens the quality of furs. In cage conditions, the quality of furs is deteriorated by increased number of foxes housed within a unit and by decreased space per individual fox. Furthermore, within-group social tension in decreased space allocation leads to a higher incidence of bite wounds in females.

In conclusion, it seems that farmed silver foxes, like their wild conspecifics, red foxes, are flexible in their living habits and capable of adapting to various kinds of social and physical environments, especially in abundant food conditions. However, the present results reveal that the foxes' natural dispersal behaviour could not be avoided, even in farming conditions. Thus, the welfare of farmed silver foxes could be improved by allowing cubs to enjoy social companionship of their family members till the onset of their natural dispersal time (i.e. September). This suggestion is in contrast to the traditional farming practice where fox cubs are weaned from their mother at the age of 7-8 weeks (June-July) and separated soon after this to live predominantly in pairs, or singly. After the onset of foxes' dispersal time, the welfare of juvenile foxes seems to be improved if they are then separated from their mother and from their littermates into pairs, or possibly to live on their own. Enlarged space as such, although permitting foxes to perform a greater amount of locomotor behaviour, does not act as the most crucial environmental factor for the welfare of farmed silver foxes. However, though it did affect negatively the habituation of foxes to humans, the enlarged space may provide foxes with some sense of control over their living environment. Furthermore, the extra space permits the provision of enriching and other welfare-promoting constructions to foxes' housing environment.

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